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**New tyrannosaur from the mid-Cretaceous of Uzbekistan clarifies evolution of giant body  
sizes and advanced senses in tyrant dinosaurs**

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**Short Title:** New mid-Cretaceous tyrannosaur from Uzbekistan

**Abstract:** Tyrannosaurids—the familiar group of carnivorous dinosaurs including *Tyrannosaurus* and *Albertosaurus*—were the apex predators in continental ecosystems in Asia and North America during the latest Cretaceous (ca. 80-66 million years ago). Their colossal sizes and keen senses are considered key to their evolutionary and ecological success, but little is known about how these features developed as tyrannosaurids evolved from smaller basal tyrannosauroids that originated in the Middle Jurassic (ca. 170 million years ago). This is largely because of a frustrating 20+ million-year gap in the mid-Cretaceous fossil record, when tyrannosauroids transitioned from small-bodied hunters to gigantic apex predators, but from which no diagnostic specimens are known. We describe the first distinct tyrannosauroid species from this gap, based on a highly derived braincase and a variety of other skeletal elements from the Turonian (ca. 90-92 million years ago) of Uzbekistan. This taxon is phylogenetically intermediate between the oldest basal tyrannosauroids and the latest Cretaceous forms. It had yet to develop the giant size and extensive cranial pneumaticity of *T. rex* and kin, but does possess the highly derived brain and inner ear characteristic of the latest Cretaceous species. Tyrannosauroids apparently developed huge size rapidly during the latest Cretaceous, and their success in the top predator role may have been enabled by their brain and keen senses that first evolved at smaller body size.

**Significance Statement:** Tyrannosaurs—the iconic group of dinosaurian carnivores that includes *T. rex*—dominated latest Cretaceous ecosystems with their colossal sizes and sophisticated senses. A gap in the mid-Cretaceous fossil record between these giant apex predators and their older, smaller relatives makes it difficult to understand how the characteristic body size and ecological habits of *T. rex* and kin developed. A new species from Uzbekistan fills this gap. This horse-sized animal shows that tyrannosaurs had yet to achieve huge size at this time, but had already evolved key brain and sensory features of the gigantic latest Cretaceous species. Tyrannosaurs apparently developed giant body size rapidly, late in the Cretaceous, and their success may have been enabled by their early-evolving keen senses.

Tyrannosaurs were at their heyday during the final ~20 million years of the Age of Dinosaurs. Iconic taxa like *Tyrannosaurus*, *Tarbosaurus*, and *Albertosaurus* reigned at the top of the food chain in Asia and North America, endowed with colossal size and sophisticated senses that set them apart from other carnivorous dinosaurs (1-2). These multi-ton, ecologically dominant latest Cretaceous species (tyrannosaurids) evolved from an ancestral lineage of basal tyrannosauroids, which originated more than 100 million years before *T. rex* but for most of their history remained second-tier predators, rarely with a mass exceeding that of a horse (2-4). The ascent of tyrannosaurs from these early species to the latest Cretaceous giants was one of the seminal events in dinosaur evolution, establishing the final dinosaur-dominated faunas that flourished before the end-Cretaceous mass extinction (5).

Little is known, however, about how tyrannosaurids developed many of their signature features, such as their gigantic sizes, highly unusual brains, ears attuned to low-frequency sounds, and extensively pneumatized skulls. This is due to a vexing gap in the fossil record that has long frustrated attempts to understand tyrannosaur evolution. There are hundreds of specimens of large-bodied latest Cretaceous tyrannosaurids (1), and now a growing record of smaller and more primitive Middle Jurassic-Early Cretaceous tyrannosauroids (2, 6-8). However, there are no diagnostic fossils from the intervening 20+ million years of the mid-Cretaceous, the time when tyrannosauroids transitioned from marginal hunters to apex predators (1-2).

We here report the first diagnostic tyrannosauroid from the mid-Cretaceous, a new species from the Turonian (ca. 90-92 million years ago) Bissekty Formation of Uzbekistan. This formation has recently emerged as one of the most important records of mid-Cretaceous dinosaurs globally (9-11). Possible tyrannosauroid specimens from the Bissekty Formation were reported more than a half century ago (12), and more recently several isolated fossils were

assigned to the group (9, 13), but none of these have been particularly complete or diagnostic at the species level, and their phylogenetic relationships have been difficult to assess. We describe a remarkably preserved and highly diagnostic braincase that links together these specimens and reveals the existence of a mid-sized species phylogenetically intermediate between the oldest, smallest tyrannosauroids and the largest, last-surviving tyrannosaurids, which had already developed many of the apomorphic features of the tyrannosaurid brain and ear but not the cranial sinus system.

### **Systematic Paleontology**

Dinosauria Owen, 1842; Theropoda Marsh, 1881; Coelurosauria Huene, 1914; Tyrannosauroida Osborn, 1905; *Timurlengia euotica* gen. et sp. nov.

### **Holotype**

ZIN PH (Paleoherpetological Collection, Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia) 1146/16, a well-preserved braincase missing only the paroccipital processes and much of the parabasisphenoid (Figs. 1-2).

### **Etymology**

*Timurlengia*, in reference to the fourteenth-century Central Asian ruler Timurleng (English: Tamerlane), and *euotica*, meaning ‘well-eared’ in reference to the large inner ear of the holotype.

### **Referred specimens**

ZIN PH 854/16, right side of a partial braincase that shares unique apomorphies with, and is otherwise identical to, the holotype (Fig. S4). We also refer to *Timurlengia euotica* a series of isolated cranial and postcranial bones described by Averianov and Sues (9) and identified as belonging to indeterminate tyrannosauroids (Fig. 1). These bones possess tyrannosauroid characters, are from the same horizon as the holotype of *T. euotica*, and belong to individuals of approximately the same body size. Furthermore, separate phylogenetic analyses place the braincase and the series of additional bones in the same position as an ‘intermediate’ grade tyrannosauroid (see Systematics). We therefore consider it most parsimonious that all of these specimens belong to the same taxon. If later discoveries show this to be incorrect, then the name-bearer of *Timurlengia euotica* is the highly diagnostic braincase.

### **Horizon and Locality**

Dzharakuduk, central Kyzylkum Desert, Navoi Viloyat, Uzbekistan. Bissekty Formation, Upper Cretaceous, middle-upper Turonian (ca. 90-92 million years ago).

### **Diagnosis**

The following diagnosis focuses on the holotype braincase only (Fig. 2). *Timurlengia euotica* is a tyrannosauroid theropod with the following autapomorphies among tyrannosauroids (those unique among all theropods are denoted by an asterisk): a diamond-shaped ventral projection of the supraoccipital that is excluded from the dorsal rim of the foramen magnum\*; extremely short basal tubera on the basioccipital, which are approximately one third the depth of the occipital condyle; a deep funnel-like otic recess (combined fenestrae ovalis and vestibuli) that widely

opens onto the lateral surface of the braincase and extends far medially into the ear region; large inner ear with robust semicircular canals\*.

### **Body size**

The holotype braincase of *Timurlengia euotica* is nearly identical in size to that of the holotype of *Xiongguanlong baimoensis* (based on nearly equal widths of the occipital condyle and supraoccipital above the foramen magnum, and depth of the paroccipital process base). Along with the phylogenetic proximity of the two taxa, this suggests that the holotype individual of *Timurlengia* was roughly the same body size as *Xiongguanlong*, whose mass has been estimated at 170-270 kilograms (14-15). Although most sutures on the holotype of *Timurlengia* are fused, part of the broken parabasisphenoid was not fused to the remainder of the braincase, perhaps suggesting that the individual was not yet osteologically mature and adults of the species may have been somewhat larger. However, almost all other tyrannosauroid specimens from the Bissekty Formation are of the same size, or smaller, than corresponding bones in the *Xiongguanlong* holotype (9). The one possible exception is a fragment of the posterior end of the lower jaw that was described as belonging to a fully grown adult, which cannot be directly compared to *Xiongguanlong* (the lower jaw of which is unknown) but is of the approximate size of the corresponding bones in sub-adult tyrannosaurids (16). Taken together, the known record of Bissekty tyrannosauroids indicates a single taxon that, at adult size, was far smaller than the derived tyrannosaurids of the latest Cretaceous.

### **Description and Comparisons**



The supraoccipital bears a pronounced midline ridge with a deep fossa on each side, as in basal tyrannosauroids (14) and close outgroups (17-18) but unlike the flatter supraoccipital of derived tyrannosaurids that expands dorsally into tab-like processes (19-20). Ventrally the supraoccipital terminates in a large diamond-shaped process that does not extend to the dorsal rim of the foramen magnum. A similar process is present in *Xiongguanlong* and tyrannosaurids but it contributes to the foramen rim (14, 20-22). The process is absent and the supraoccipital is broadly separated from the rim in *Guanlong* and *Dilong* (20), whereas non-coelurosaurian outgroups have a tiny squared-off projection that enters into the rim (17-18) and more derived coelurosaurs such as dromaeosaurids have a supraoccipital that broadly contributes to the foramen magnum (23). The supraoccipital is solid internally and lacks the enlarged extensions of the posterior tympanic recesses that fill the bone in tyrannosaurids, including juveniles (20, 24-26).

The bases of the paroccipital processes are entirely hollowed out by enormous posterior tympanic recesses. Only coelurosaurs possess such extensive recesses (20, 27), as outgroups have either a tiny sinus penetrating the anterior edge of the paroccipital process (28) or lack a recess in this region altogether (29-30). There is a deep fossa on the posterior surface of each paroccipital process, lateral to the foramen magnum, as in basal tyrannosauroids such as *Guanlong* and *Dilong* but not in tyrannosaurids (2, 20). A paracondylar pocket housing three foramina—two for cranial nerve XII and a multipurpose vagal foramen for nerves X and XI and associated features—invades the otoccipital and basioccipital dorsolateral to the occipital condyle. The pocket is shallow as in basal tyrannosauroids, not deeply concave as in tyrannosaurids (2, 20). There is no such pocket in dromaeosaurids and other derived

coelurosaurs, in which the nerve foramina are flush with the external surface of the otoccipital (23, 31-33).

The basal tubera are autapomorphically small. This is an extreme version of the basal tyrannosauroid condition, in which the basal tubera are shallower than the occipital condyle, in contrast to the longer tubera of tyrannosaurids (2, 20) and derived maniraptorans (23). The basioccipital is not invaded by a subcondylar recess: the interior of the bone is solid and there are no large pneumatic foramina ventrolateral to the occipital condyle. This recess is characteristic of derived tyrannosaurids (20, 26) and other coelurosaurs (27), but is absent in *Xiongguanlong* (14) and other basal tyrannosauroids (2, 20). As in most theropods, there is a deep basisphenoid recess on the ventral surface. Its internal structure is complex: posteriorly it is divided into two large ovoid chambers and anteriorly it is traversed by many small bony struts. Anterior to the recess much of the parabasisphenoid is missing, as indicated by an open crescentic suture.

A thick crista tuberalis (=metotic strut) separates the posterior and lateral surfaces of the braincase. In posterior view, the width across the opposing cristae is greater than half the depth of the braincase as in *Guanlong*, *Dilong*, and *Xiongguanlong*, but unlike the narrower cristae in tyrannosaurids (20), other coelurosaurs (23, 31-33), and outgroups (17-18). The otic recess (=columellar canal) is a deep funnel whose wide external opening trends medially into the braincase interior, where it is divided into a pneumatopore supplying the posterior tympanic recess and the fenestrae vestibuli and pseudorotunda. A deep otic recess with an internal fenestra vestibuli is characteristic of tyrannosauroids (20, 26), and *Timurlengia* is most similar to *Dilong* in having a large external opening of the recess, whereas in tyrannosaurids the recess is partially concealed by the superficial lamina of the prootic (20).

Extending anterodorsal from the otic recess is a pronounced otosphenoidal-antotic crest on the lateral braincase surface, as in derived tyrannosaurids (2). Anteroventral to this crest are three prominent foramina: one opening for cranial nerve VII and separate openings for the ophthalmic and maxilla-mandibular branches of cranial nerve V. There are no pneumatic foramina in this region. This structure is common among theropods but differs from the highly derived condition of tyrannosaurids, in which a deep prootic fossa houses the nerve openings and a pneumatopore leading into the anterior tympanic recess (20). The trigeminal nerve (V) emerges from the endocast as a single stalk and bifurcates within the prootic, as is typical for theropods but differing from tyrannosaurids in which the two branches arise from the endocast separately (20, 26). A small portion of the prootic is filled by what may be part of the anterior tympanic recess, but this sinus was probably mostly within the missing parabasisphenoid.

The brain endocast is strikingly similar to those of tyrannosaurids, particularly *Alioramus* (20, 26, 34-35). There is only a slight midbrain flexure, resulting in a fairly shallow endocast that would have been tubular if complete. This is a synapomorphy of tyrannosauroids (26), differing from the deeper and more flexed (S-shaped) endocasts of non-coelurosaurian (26, 29) and coelurosaurian (31-32) outgroups. There is a pronounced midbrain peak (probably related to the transverse and longitudinal venous sinus) anterior to the posterior middle cerebral vein, which is present in tyrannosauroids but absent in most outgroups (20, 26). The flocculus is indistinct and barely crosses the plane of the anterior semicircular canal, as in tyrannosauroids and non-coelurosaurs but contrasting with the enlarged bulbous shape in more derived coelurosaurs (20, 26).

The inner ear endocast is triangular in lateral view with an expanded anterior semicircular canal, as is typical for theropods (26, 29). The semicircular canals and cochlear duct are

extremely robust compared to all other theropods with comparative CT data, including both juvenile and adult tyrannosaurids (20, 26, 29). This is an autapomorphy of *Timurlengia* whose functional implications are unclear, but it could potentially be related to increased agility (36). The cochlear duct is elongated, such that it extends far ventral to the brain endocast and is approximately as long dorsoventrally as the depth of the semicircular canals. A long duct is a synapomorphy of tyrannosauroids (20, 26), different from the much shorter ducts of most other theropods, and would have increased sensitivity to lower-frequency sounds (37-38) and may possibly have been related to complex vocalizations and sociality (38).

## **Systematics**

To test the phylogenetic relationships of *Timurlengia euotica* broadly among theropods, we added it to the most recent version of the Theropod Working Group dataset (33), which includes a wide sample of coelurosaurs and outgroups scored for over 850 anatomical characters.

We first ran an analysis in which only the holotype braincase was used to score *Timurlengia*, which resulted in 99999 most parsimonious trees (the memory limit of the program; individual trees: length=3364, consistency index=0.322, retention index=0.777). The strict consensus places *Timurlengia* as an intermediate-grade tyrannosauroid, nested between the basal proceratosaurids and the derived large-bodied tyrannosaurids (Fig. S5A). We then undertook a second analysis in which *Timurlengia* was scored based only on the series of referred specimens described by Averianov and Sues (9). This produced 99999 most parsimonious trees (length=3367, consistency index=0.322, retention index=0.777), the strict consensus of which (Fig. S5B) recovered *Timurlengia* and *Xiongguanlong* as a sister-taxon pair of intermediate-grade tyrannosauroids. Finally, we ran a third analysis in which *Timurlengia* was

scored based on the holotype braincase and all additional material described by Averianov and Sues (9). This produced 99999 most parsimonious trees (length=3367, consistency index=0.322, retention index=0.777), the strict consensus of which (Fig. 3) places *Timurlengia* as an intermediate tyrannosauroid, immediately outside the clade of *Xiongguanlong* and tyrannosaurids.

We interpret these results as supporting two main conclusions. First, the braincase and referred specimens belong to the same taxon, given their nearly identical phylogenetic placement when run separately and the absence of any fossils indicating the presence of more than one tyrannosauroid taxon in the Bissekty Formation. Second, this taxon, *Timurlengia euotica*, is an intermediate-grade tyrannosauroid that is phylogenetically proximal to *Xiongguanlong*, and the two may or may not form their own distinct subclade.

## **Discussion**

The discovery of the braincase ZIN PH 1146/16, with its unambiguous tyrannosauroid features but lack of synapomorphies of large-bodied tyrannosaurids, helps tie together disparate specimens of small tyrannosauroids found over many years in the Bissekty Formation of Uzbekistan (9, 12-13). It reveals the presence of a new taxon that fills a major gap in the evolutionary history of tyrannosauroids, which has long frustrated attempts to understand the phylogeny and evolution of these most iconic of dinosaurs. Critically, the new taxon, *Timurlengia euotica*, is the first diagnostic tyrannosauroid from the middle part of the Cretaceous, an approximately 20-million-year window spanning the end of the Albian to the early Campanian. Previous reports of tyrannosauroids from this interval have been limited to fragmentary and undiagnostic specimens (12-13), have uncertain ages and may be from the latest

Cretaceous (39), or are specimens whose ages are poorly constrained and whereabouts currently unknown (40).

*Timurlengia* helps clarify trends in tyrannosauroid body size evolution, particularly the origin of colossal sizes in latest Cretaceous tyrannosaurids, which at 10+ meters long and 5+ tons in mass were among the largest carnivores to ever live on land. Tyrannosauroids ascended into an apex predator role sometime in the middle Cretaceous gap, as the last-known species before the gap, about 100-125 million years ago, were about the size of a horse and the first ones appearing after the gap, about 80 million years ago, are gigantic taxa such as *Lythronax* and *Gorgosaurus* (2-3). The new mid-Cretaceous Uzbek taxon is also approximately horse-sized, far smaller than the end-Cretaceous giants. Although it is currently only a single data point, *Timurlengia* indicates that tyrannosauroids remained small-to-medium-sized well into the middle Cretaceous, during a time when late-surviving large allosauroids remained at the top of food chains in Asia and North America (41-43). Tyrannosauroids apparently developed huge size and ecological dominance suddenly, sometime around the start of the Campanian, but the trigger remains unclear. It is tempting to speculate that the Cenomanian-Turonian extinction event ca. 94 million years ago may have played a role, but this may have occurred many millions of years before the allosauroid-tyrannosauroid turnover. Unfortunately, the currently poorly known mid-Cretaceous fossil record makes testing extinction and radiation scenarios difficult.

The new Uzbek taxon is an intermediate tyrannosauroid, within the grade of species between the oldest and most primitive proceratosaurids (*Guanlong*, *Proceratosaurus*, and kin: 6-8) and the derived, large-bodied tyrannosaurids (*Tyrannosaurus*, *Albertosaurus*, and kin: 21-22, 25). *Timurlengia* shares many similarities with another intermediate taxon, *Xiongguanlong* from the Aptian-Albian of western China, which is the last-known diagnostic tyrannosauroid before

the mid-Cretaceous gap (14). Their braincases are almost identical in size, they possess nearly identical diamond-shaped ventral processes of the supraoccipital (differing only in whether the process makes contact with the dorsal rim of the foramen magnum), and both have short basal tubera without large external pneumatopores leading into a subcondylar recess. Furthermore, one of the referred specimens of *Timurlengia* is a gracile and elongate maxilla, remarkably similar in proportions to that of the long-snouted *Xiongguanlong*. We hypothesize that these two taxa, and potentially a long-snouted skull from the Bayan Shireh Formation previously assigned to *Alectrosaurus* but unavailable for study (40), belong to a grade or clade of longirostre tyrannosauroids immediately outside of the clade of derived, large-bodied, latest Cretaceous forms. This mid-sized, long-snouted bauplan may have been the ancestral stock from which the gigantic tyrannosaurids arose.

The holotype braincase of *Timurlengia* is a keystone specimen for understanding how the highly derived brains, sensory organs, and endocranial sinuses of large-bodied tyrannosaurids evolved. Braincase material is known for only a few other basal tyrannosauroids, but has yet to be CT scanned or studied in detail, making *Timurlengia* the oldest and most basal tyrannosauroid with a well-documented braincase. Aside from its autapomorphically robust inner ear, the brain of *Timurlengia* resembles a smaller version of the brain of *Gorgosaurus* or *Tyrannosaurus* (25-26). It reveals that many apomorphic features of the tyrannosauroid brain and ear were already present in mid-sized, non-tyrannosaurid taxa, including a tubular endocast with a slight midbrain flexure, a pronounced midbrain peak, and an elongate cochlear duct. It has been suggested that some of these features may have been instrumental in the evolutionary success of the large-bodied, latest Cretaceous tyrannosaurids, particularly the long cochlear duct that imparts heightened ability to hear lower-frequency sounds than in other theropods, which would have

been useful for an apex predator (2, 26). These features, however, developed long before large body size. In this regard, the brains and keen senses of early tyrannosauroids may have predisposed them to become successful apex predators when the opportunity arose.

On the other hand, the pneumatic sinuses of *Timurlengia* are nowhere near as elaborate as in the largest tyrannosaurids. The baseline sinus system of coelurosaurs is present, but *Timurlengia* lacks the supraoccipital and subcondylar recesses so characteristic of tyrannosaurids, and also seemingly possesses a less extensive anterior tympanic recess in the prootic. It may be that these recesses developed in concert with large body size, either to lighten the skull or, in the case of the tympanic sinuses, to help tyrannosaurids maintain the ability to hear lower-frequency sounds at larger size (26).

## **Conclusions**

*Timurlengia* is a long-awaited diagnostic tyrannosauroid from the middle part of the Cretaceous. It indicates that these predators were still far from giants during this time, but had already evolved signature brain and sensory features that may have been tied to the extraordinary success of the last-surviving, latest-Cretaceous species like *Tyrannosaurus*. However, *Timurlengia* remains a single data point from a still murky interval in dinosaur history, and future discoveries from this gap will undoubtedly lead to a better understanding of how tyrannosauroids rose from marginal creatures into some of the largest terrestrial predators in Earth history.

## **Materials and Methods**

To visualize and study the internal structures of the braincase, ZIN PH 1146/16 was subjected to an x-ray computed microtomography scan at the School of GeoSciences, University of



Edinburgh ( $\mu$ CT instrument constructed in-house). Data were acquired using a Feinfocus transmission x-ray source at a peak energy of 120kV and a Perkin Elmer XRD0822 flat panel x-ray detector using 3000 exposures of 2 seconds each and an aluminium energy filter. Octopus v8.7 was utilized for tomographic reconstruction. The final slice datasets were imported into Mimics v.17 for segmentation and digital reconstruction.

To assess the phylogenetic relationships of *Timurlengia euotica*, we added it to the data matrix of Brusatte et al. (33), which is the latest iteration of a 20+ year research program (Theropod Working Group [TWiG]) that has been building progressively larger datasets of theropod phylogeny based on direct examination of specimens. The dataset includes 153 taxa scored for 853 discrete morphological characters, representing a broad spread of theropods and their anatomical features. Three versions of the analysis were run in which *Timurlengia* was scored based on: 1) the holotype braincase only; 2) the series of specimens described by Averianov and Sues (9) only; 3) both the braincase and the series of referred specimens. In each case the matrix was run in TNT (44) under maximum parsimony. We first employed a “new technology search” in which the shortest tree was found in 10 replicates, and then those trees were subjected to a “traditional” round of tree bisection and reconnection branch swapping. For further details, see *SI Appendix*.

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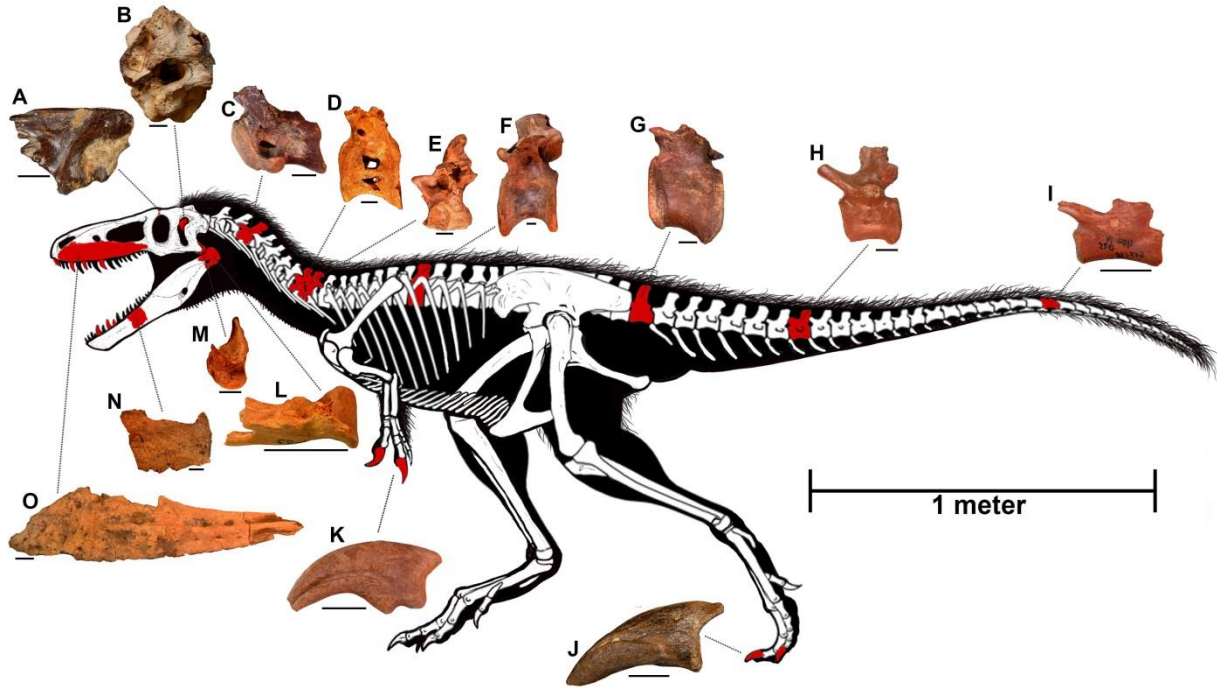


Fig. 1. Skeletal reconstruction of *Timurlengia euotica*, with known bones colored in red.

Individual bones come from different individuals, as they were surface collected as isolated specimens in the Bissekty Formation of Uzbekistan. The proportions of the skeleton are based on an intermediate body type between *Xiongguanlong* and *Tyrannosaurus*, but should be considered provisional until associated material is found. (A) Left frontal, ZIN PH 2330/16. (B) Holotype braincase, ZIN PH 1146/16. (C) Cervical vertebra, ZIN PH 671/16. (D) Cervical vertebra, USNM (National Museum of Natural History, Smithsonian, Washington, USA) 538131. (E) Dorsal neural arch, USNM 538132. (F) Dorsal vertebra, CCMGE (Chernyshev's Central Museum of Geological Exploration, Saint Petersburg, Russia) 432/12457. (G) Anterior caudal vertebra, ZIN PH 951/16. (H) Middle caudal vertebra, ZIN PH 120/16. (I) Distal caudal vertebra, ZIN PH 507/16. (J) Pedal ungual, USNM 538167. (K) Manual ungual, ZIN PH 619/16. (L) Right articular and surangular, ZIN PH 1239/16. (M) Left quadrate, ZIN PH 2296/16. (N) Right

dentary, ZIN PH 15/16. (*O*) Right maxilla (reversed), ZIN PH 676/16. (Individual scale bars, 2 cm.) Artwork by Todd Marshall.



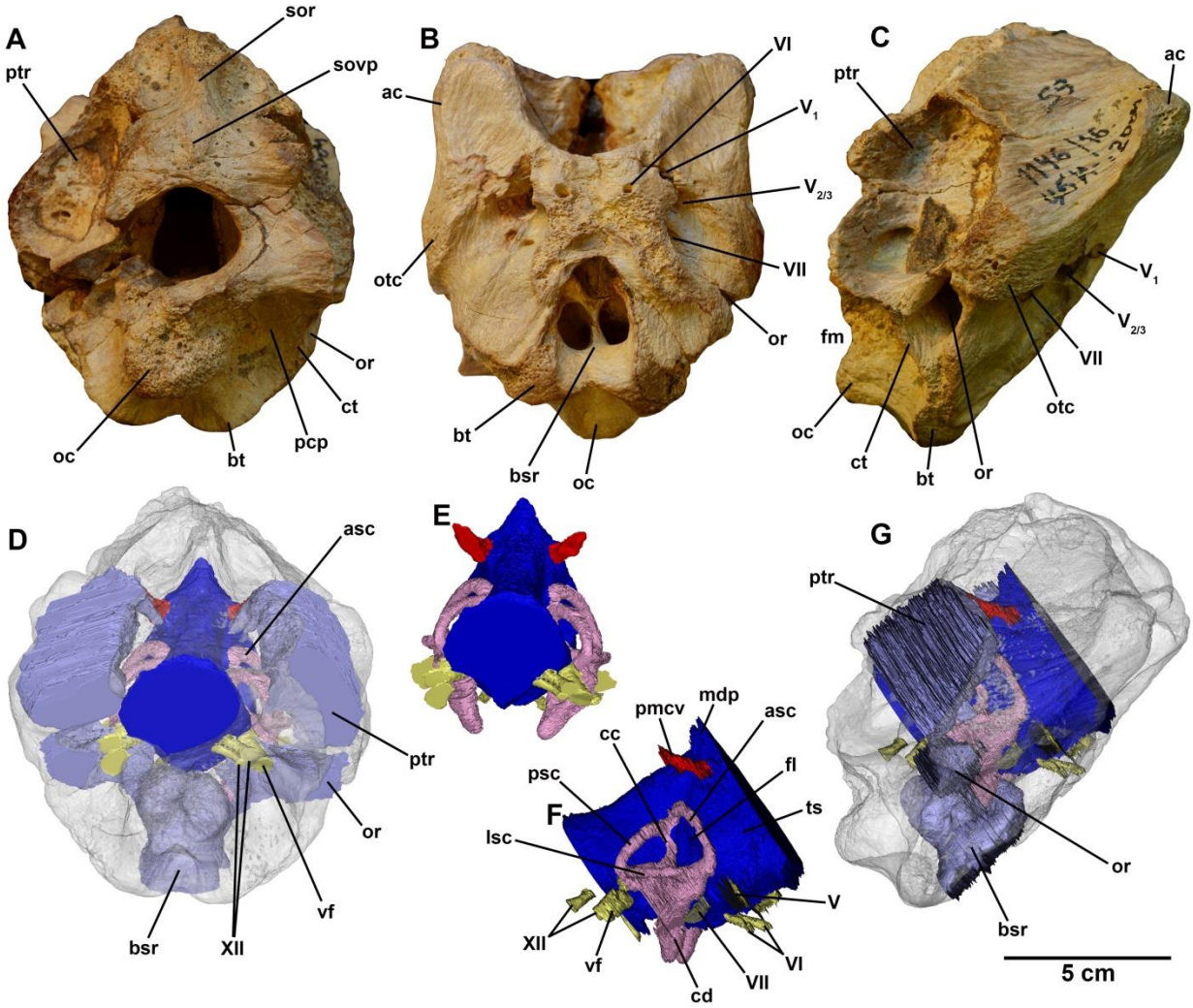


Fig. 2. Holotype braincase of *Timurlengia euotica* (ZIN PH 1146/16). (A) Posterior view. (B) Anterior view. (C) Right lateral view. (D) CT reconstruction in posterior view. (E) CT reconstruction of endocast, ear, nerves, and vessels in posterior view. (F) CT reconstruction of endocast in right lateral view. (G) CT reconstruction in right lateral view. Abbreviations: ac, antotic crest; asc, anterior semicircular canal; bsr, basisphenoid recess; bt, basal tubera; cc, common crus; cd, cochlear duct; ct, crista tuberalis; fl, flocculus; fm, foramen magnum; lsc, lateral semicircular canal; mdp, median dural peak; oc, occipital condyle; or, otic recess; otc, otosphenoidal crest; pcp, paracondylar pocket; pmcv, posterior middle cerebral vein; psc, posterior semicircular canal; ptr, posterior tympanic recess; sor, supraoccipital ridge; sovp,

supraoccipital ventral process; ts, transverse sinus; vf, vagal foramen. Roman numerals designate cranial nerves.

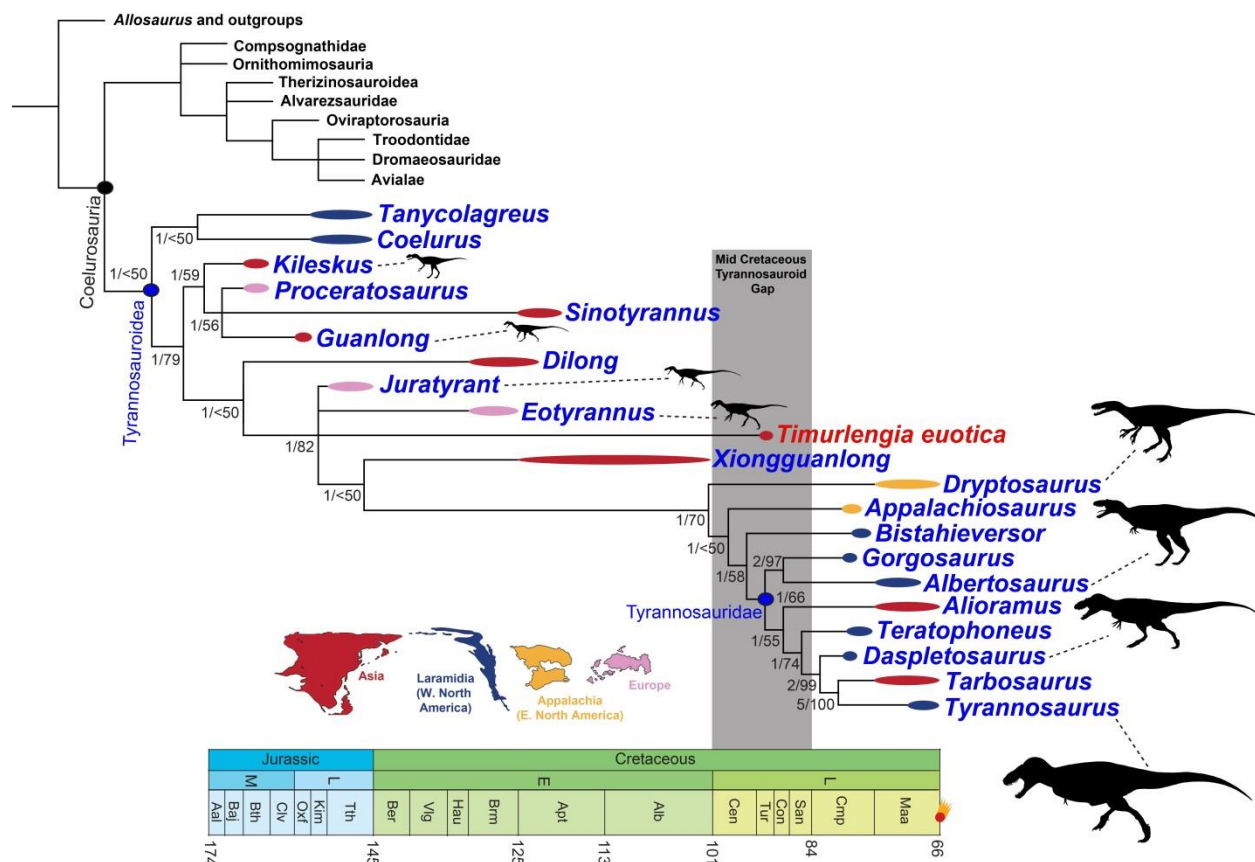


Fig. 3. Phylogenetic relationships of *Timurlengia euotica* among theropod dinosaurs. Strict consensus of 99999 most parsimonious trees (length=3367, consistency index=0.322, retention index=0.777) recovered from cladistic analysis in which *Timurlengia* is scored based on the holotype braincase and series of referred specimens. Numbers next to nodes are Bremer/jackknife support values, thick lines next to each taxon depict temporal range (which in most cases is age uncertainty and not true range), colors of lines denote geographic areas, and silhouettes are in relative proportion and scaled to total body length (*T. rex* = 13 meters). Geographic silhouettes from Loewen et al. (3) and taxon silhouettes from phylopic.org (*Kileskus*: T.M. Keesey; *Guanlong*: S. Hartman; *Juratyran*: S. Hartman, T.M. Keesey; *Eotyrannus*: S. Hartman; *Dryptosaurus* T.M. Keesey; *Albertosaurus* C. Dylke; *Daspletosaurus* S. O'Connor, T.M. Keesey; *Tyrannosaurus* S. Hartman).

## **SUPPLEMENTARY APPENDIX**

- 1) Materials and Methods
- 2) Supplementary Figures S1-S5
- 3) Phylogenetic Dataset
- 4) Supplementary References

## **1) Materials and Methods**

*Timurlengia euotica* was added to the phylogenetic dataset of Brusatte et al. (2014), the latest iteration of the Theropod Working Group dataset, which includes 853 characters scored for 153 taxa. A few other changes to the dataset were made: 1) *Incisivosaurus Guanlong*, *Dilong*, *Alioramus*, *Daspletosaurus*, and *Tyrannosaurus* were scored as state 1 for character 7. 2) *Sinraptor* was scored as state 1 for character 18; 3) *Xiongguanlong* was scored as state 1 for character 609. The complete dataset is provided in Section 3 of the Supplementary Appendix.

Three separate phylogenetic analyses were run, differing only in how *Timurlengia* was scored: 1) based on the holotype braincase only; 2) based on the referred specimens described by Averianov and Sues (2012) only; 3) based on the holotype braincase and the referred specimens.

In each case, the dataset was analyzed with equally weighted parsimony in the phylogenetic program TNT v. 1.1 (Goloboff et al. 2008). Following previous TWiG protocol, the outgroup *Allosaurus* was used to root the tree. Because of the large size of the dataset a heuristic search strategy was necessary. First, the data matrix was analyzed under the “New Technology” search options, using sectorial search, ratchet, tree drift, and tree fuse options with default parameters. The minimum length tree was found in 10 replicates, a procedure samples as many tree islands as possible. The generated trees were then analyzed under traditional TBR branch swapping, which aims to more fully explore each tree island. Zero-length branches were collapsed following Rule 1 of Coddington and Scharff (1994).

Strict consensus topologies were constructed for each analysis after exclusion of five wildcard taxa: *Kinnareemimus*, *Epidendrosaurus*, *Pyroraptor*, *Hesperonychus*, and *Limenavis* (see Brusatte et al. 2014). The degree of support for individual clades was assessed in two ways: Bremer support values (=decay indices, the number of extra steps required for the clade to fall apart in the strict consensus of less optimal topologies) and jackknife percentages (the percent of trees which includes the clade in question recovered in a jackknife analysis, with 36% character removal probability and 500 replicates).

## 2) Supplementary Figures

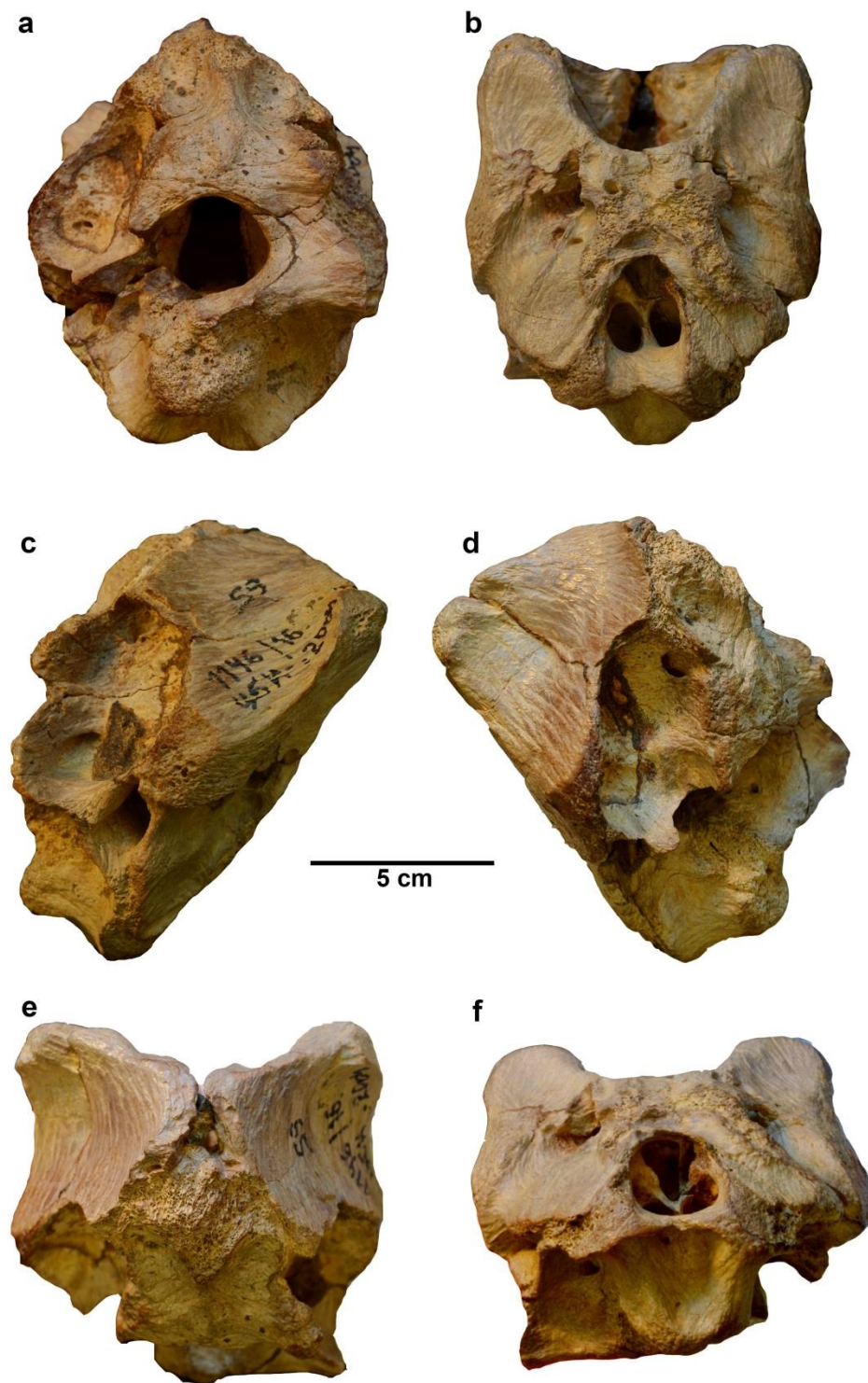


Fig. S1. Holotype braincase of *Timurlengia euotica* (ZIN PH 1146/16). (A) Posterior view. (B) Anterior view. (C) Right lateral view. (D) Left lateral view. (E) Dorsal view. (F) Ventral view.



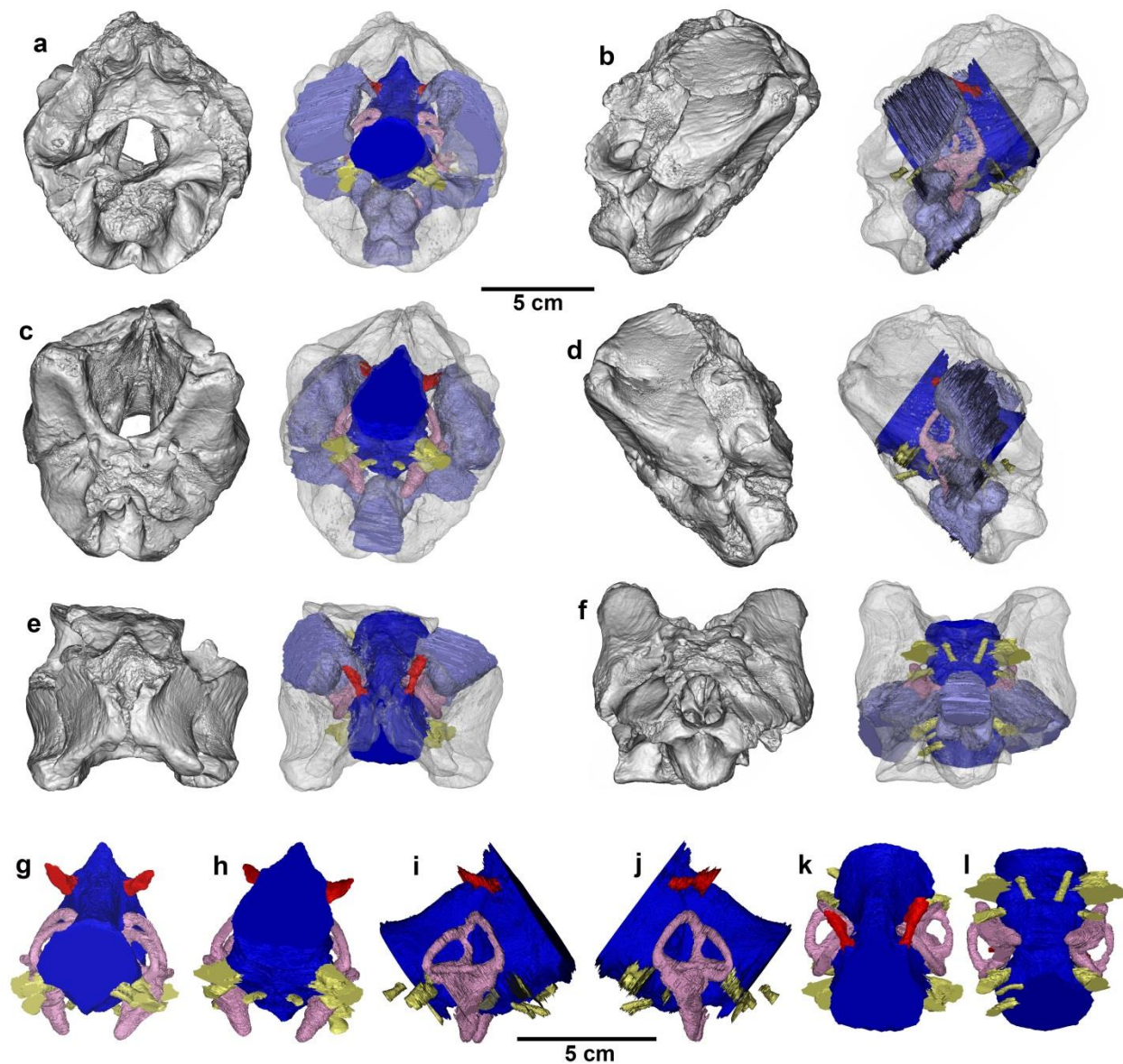


Fig. S2. CT reconstructions of the holotype braincase of *Timurlengia euotica* (ZIN PH 1146/16). (A) Posterior view. (B) Right lateral view. (C) Anterior view. (D) Left lateral view. (E) Dorsal view. (F) Ventral view. Endocast in : (G) Anterior view. (H) Posterior view. (I) Right lateral view. (J) Left lateral view. (K) Dorsal view. (L) Ventral view.

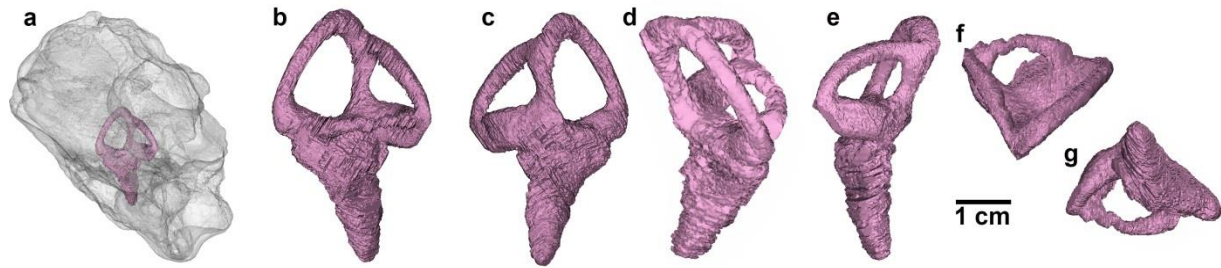


Fig. S3. Left inner ear of the holotype braincase of *Timurlengia euotica* (ZIN PH 1146/16). (A) Left lateral view of skull with ear in situ. (B) Lateral view. (C) Medial view. (D) Anterior view. (E) Posterior view. (F) Dorsal view. (G) Ventral view.



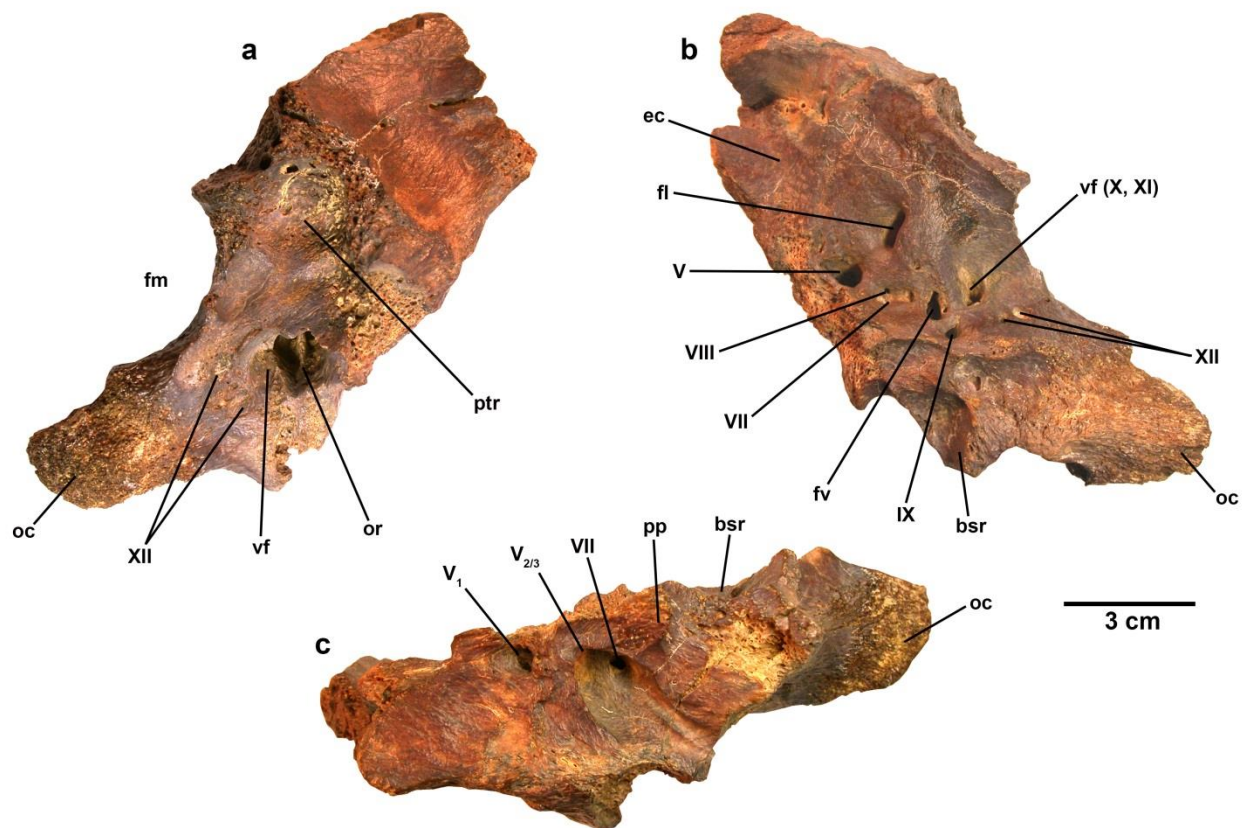


Fig. S4. Referred partial braincase (fragment of the right side of the braincase) of *Timurlengia euotica* (ZIN PH 854/16). (A) Right lateral view. (B) Medial view. (C) Ventral view. Abbreviations: bsr, basisphenoid recess; ec, endocranial cavity; fl, flocculus; fm, foramen magnum; fv, fenestra vestibuli; oc, occipital condyle; or, otic recess; pp, preotic pendant; ptr, posterior tympanic recess; vf, vagal foramen. Roman numerals designate cranial nerves.

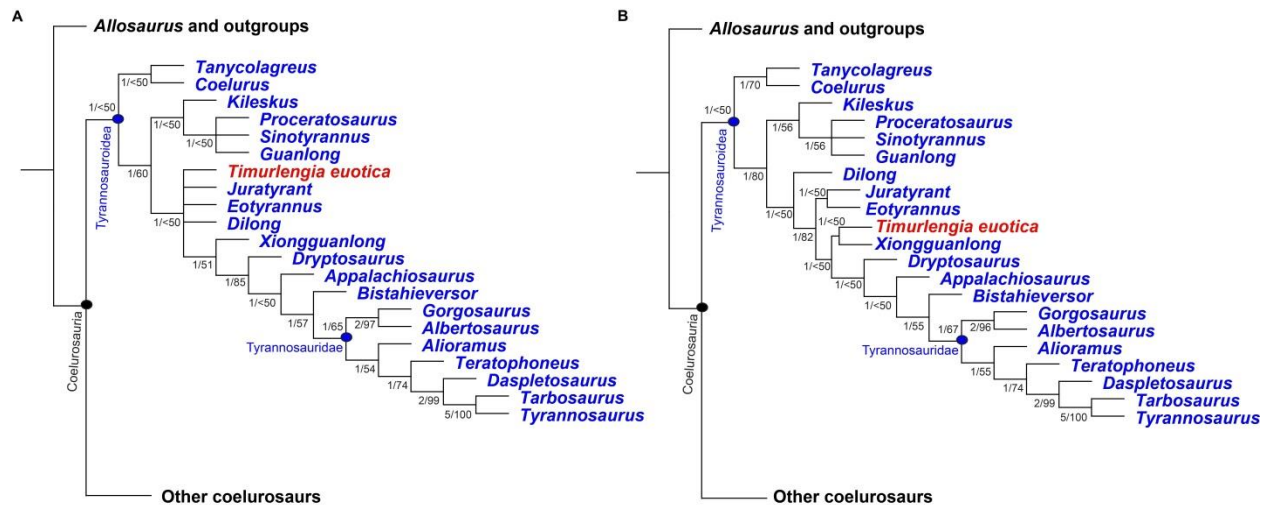


Fig. S5. Results of phylogenetic analyses to determine the placement of *Timurlengia euotica* (ZIN PH 1146/16). (A) Strict consensus of 99999 most parsimonious trees (length=3364, consistency index=0.322, retention index=0.777) recovered from cladistic analysis in which *Timurlengia* is scored based on the holotype braincase only. (B) Strict consensus of 99999 most parsimonious trees (length=3364, consistency index=0.322, retention index=0.777) recovered from cladistic analysis in which *Timurlengia* is scored based only on the series of referred specimens described by Averianov and Sues (2012). In both cases, numbers next to nodes denote Bremer/jackknife support values.

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Tianyuraptor\_ostromi

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Anchiornis\_huxleyi

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001???0?00????000??030000?000????????0?????0???0?????0?????00000?0000[01]0?  
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Xiaotingia

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Aurornis

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Eosinopteryx

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Troodon\_formosus

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Sinovenator\_changii

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EK\_troodontid\_IGM\_100/44

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IGM\_100/1126

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1?010?020020200010131012??111000????0??2?001210001?00000011?00?0?020000?00100?1?  
00000111?01?0?00?000003?????000000????00?00?00?0?0?0000?00?00???0?0????????0  
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IGM\_100/1323

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Archaeopteryx\_lithographi

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2111010?12003020121022?2?2?111100000?0001000000030?0000000001100000??00?0001100  
11100001001?01000000??0000?030000?0000000?00110??00?0??000?00??000??00?0000000  
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Confuciusornis\_sanctus

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?10?0000?110?00000??1?00?0000?0?01?0?10100?00?????????1??00?0???0000000??000??0  
1?02??00100000?0??????000?000??0????????????????????????????????00010??0?0?  
?00??10?????????????0??????0001?000??0??0?00111?0?1?000?100?????0??0??1?????????  
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Jeholornis\_prima

10????0???????1??0??0??0??001?????????????????0??????????0000?1??00?00?1  
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01?0???2???1?221?10??????01????0101101003000000000?0??1000?00?010???1??000?1?  
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1??0000?00000?0?1000120001000?0010000?000?0000?00001000010110000?000000000000?  
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Jixiangornis\_orientalis

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10212000020101?221?10?2?11?001??1?01[12]1101003000?00?000?0??1000?00?0100??11?  
001?1?????????00?000000?12300?00010?????????????????????0?????000?00?0000?11?0?10  
?11?0?????0000000000?0010011210010?0?0000000?000??0?0?0??0?010?00100??0000?00  
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0100??0?????0?????????????1???

Yanornis\_martini

?00???????????????1?010?????0?11??0??2??0?????00?????????0000011??0?????  
00?1??00?0?0???1??0?????????4?1??????04??????110?011031110?011?130010?????????  
?????????????23?010?2??10??1??0?0121[23]0000300000?0001??00?0??????0???21?1?0????  
?????????????0?????300100012?????????10??????1?????????????????0?0011?00??0210?[  
12]??10100001010?1?11?112100111??0101?0101?10000?0?????021[01]101311[01]1100[01]10  
0?0?1?0?0?00?????0?00?1110[01]?1?00??1?0??01100?????????01??1???????1100?11?001  
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??0??100000?00?1??0?????????????00?????????0????000?????0??????000?00?????????  
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### Patagopteryx\_deferrariisi

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00????0101?1210[01]00??[01]?10?0??01000001[01]0001?[12]00??30?????00?2000000?0  
10120????0?000[12]11001100000?[01]?0??0?100?1?200??01?0??0?001??????00??0?1???  
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????0?0?0?110????????????????0????????????????????0020000?00????????0?0  
?00?0001?00000??????00111?00100??????1?0000??????0100?0?0?0?000??00??0?  
????00?0?0?1?????0?10????????00??010?????00000000?0?????000000??00?1???00  
000010?????1??0???0???0?1???10?

### Cathayornis

?0?????????????????1?010????0?1????????0????????????????00????????????00  
001?????0??????[02]??????3????2???4??0??11?02?1031110?011?1300?0?0111?0?0  
0?12000?201?1022?23??????1??0??[12]1[01]1?0?3000?0??00????0??1??0?0100??111?  
????????0?0?0????0???2300[01]0?012????????????????????0?0????0???0111?001  
0?20??1??10110?101???010?01200010010110[01]?01020111110?[01]?1????210120?11?01?  
0101011?0?000001??1?0?0?1[01]1?0????????0?01110??????01??????01????????0?  
??110?00000????????0?0?0100?10100?000????????????0????????0?00??????????  
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### Concornis

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00101?0?0010001?0??[01]001?110??0102?1???10??1[01]1?[12]????????????[01]??????  
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### Gobipteryx

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0?0?100012000[12]001?1?0110??0????????1?121??[012]0????1?0??1??????000?0??1  
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#### Vorona

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#### Songlingornis

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#### Pengornis\_houi

?0010????????10010?0?00?????0?12?0????0????0????000?001?????  
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1[01]00?00?????0?1?012111[01]0?011010001[01][01]1????1?1???10[12][12]0??1?1?1?  
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#### Hesperornis

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?1??01000??021023?03?12???0001??11?1213110010?0?00?01?1?0000?000??00??2??1?11  
11????0??????10000??10?1?10?1121200110?1010??1110011100?00?0???101012101100001  
2?0?000100100?0??10?0???00011?0?0????????0?0?0?0?0????????????20?110  
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000?????????0?1?0100?0?0???00????????0?0?0?0?0????????0?00????????????00?0?0??

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Lithornis

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10101?20200102??2102?????12?01000??11?12130100????0??200?01?2010??0?0?0??21??  
?12??????????00??00000??300?11212100?00011111010110?11[01]1101?1111?01?10121012  
?0111[12]1211122110100?01011011110112101111100110001[12]1110000101010101111131  
30110[01]11102[01]0120110?11211020110002111122210010[01]?000011?1???????011?111?  
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Hongshanornis\_longicrest

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000?????????1???1100??[01]?00??2?0??1????????????????????????0100?11??001?11?????0?  
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Liaoningornis\_longidigitu

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Crypturellus\_undulatus

10????012?020002?2001010100?00?111?12002100001011100010???1?10000?000??10  
2?001?1?????????1110111122100?01107?110??12?24??121?11010010311011011113003??001  
210001?202201120021023?23?12?01000100110121301?0???01000200001?20000200?0?00102  
1???120??01?????0???00000103002112121[01]010001111101011001101111111100101012  
10101121121211112?101000210110101111121001111101100012011000011101010111110314

01011111020?120110?11211020211002111122210010110?011?10102000001111110000??11  
00?10?01??11??  
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Gallus\_gallus

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21101?1?????????101[01]1111221?0?01007?120??12?24??1[12]1?11012010311020011113003  
??001211111?2?2001120021023?23?12?0100011011??213010010001000200100?20100200?0?  
0???21???121?01???0?00??000001030011021212111112211011111111111011000110101  
11210101120111211112110100021011111111121001111101100012011000010111010111111  
31401001211021?121111?112110202110021111322200111?00?0110001020?000111111?000?  
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Crax\_pauxi

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21101?1?????????1000111122100?111?7?120??12?24??121?11002010311121011113003??000  
2100?1?2?2001120021023?03?12?0100011011?12130100100010002001?1?20100200?0?0???2  
1???121?01?????00??00000103002102121211112211011111111111101100011010111210  
1011201112111121101000210111111111210011110110001201100001011101011111131401  
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Anas\_platyrhynchus

100???102?021002?2101001100?00?111?10002??00?1?100010?0???1?10200000100?02  
1101?1?????????101?1111221?0?011?7?11???10?2410121?11011110311111011113003??0012  
000?1?2?2001120021023?13?12?0100011011?121311?0???010002101?1?20100?00?0?0?1021?  
??121?????????00??000001130021021211111122110211121111110110001111011121010  
1020111211113120100101010?1[01]11111210001110011000120110000101110111111123140  
1010111021?111110?111110102110021111[23]2210010210?0011?10?020?000111111?000??0  
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Chauna\_torquata

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21101?1?????????1011101112100?111?7?11???1012412111?10000010311111011113103??001  
2101?1?2?200102?021023?23?12?0100011011??213010010000000200101?20100000?0?0?102

[illegible]

0102?00010?100?????0000000000100001??0000??0000101?1100??0000?????????????  
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Citipati\_osmolskae

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010111?1?????????1011101100101211001??201??002200111?0111200110100100?110000010  
00211001??02012020??10111111?2101000000000?0000000000000000000011020000000?0?00  
1000?000002011??0?0??[01]0000200012200010000000001102?1??0000??0000010001010?0000  
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0201???2?1?0000000????0????????????????????????????????????10???00?00?????????????  
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Oviraptor\_philoceratops

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?1?1?????????????????????????????????0?????????????????12??1?????00???10?00?00??1??0???  
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010?0?00?0?0???1?100??????1100???0????????00?????????000?0?00000?????????????????  
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?0?01??????01?????????????0????0???00?0?0?0?00?000?00????????????????????0?0??  
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Microvenator\_celer

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Caudipteryx\_zoui

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Ingenia\_yanshani

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?1????????????????????????????????1??01???2?00??1011120011??00000??100000100021?????  
02012020011011?11101101?0000?00011?000000000?0000??11?2000?000?0?001000??????  
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2?????0101?0?0?0??0?0?0101000?????1100??00?0?????????????????00??0?00?00?000?0  
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0010??1?1?0?0????10??0??0?0?000??11??0??010000000100000000?000100?0000000  
10?????????0?1?0??00?1??1??

Rinchenia\_mongoliensis

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11?1????????????????1?????????????0????220?????????2??1??00?0??1?0001000?1????  
1????????????????1?????????0??0?0?0?0?????0?00?0001??2?00?????????????0?0??00??  
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Conchoraptor\_gracilis

??010?????????1??00111?1???1?11?000??21000110?00????1?0????121120?010?0?0  
111?1?????????01010110010??1?012?110??10??01?1????20011000010??????001000210  
0010102002020??101101[01]1?11010000?00010000010?000??000?001102?0?0000?0?001000  
1000002001??????0?0?0200012?????0000000000????????10??0100100???????000?0?010?  
??00?00?  
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01????1?000?1?0?0?01?11?0?0?01????0?2????????0??0?0?00?0?0?0?01?00??0?00?000?0?  
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Chirostenotes\_pergracilis

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??1?????????????????1101?12?????1?12???0?????????????????101?1?????????00?100021?00101  
022120201110?111[01]??01??100??00?100000200000?000?0?1??20?0?000?0?00100??????  
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Avimimus\_portentosus

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11?????????????011010110101?1?00??100?????????????????????????0100?????????00?211?01  
??0201202010?011?0?1000100?0??00011110020??00?0?0?01?02?000000?0?001000??????  
?0?????????00?01??0?02001?????????????????0??0??00?0?0?????????02001000????????  
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00020?0100000000000000?00?01??0?????0?0?????????????????????????????1?0??????????  
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01000001??????????????00001??????101001??0101?0100?0?000??001000?00?0?????0?0?1  
001??101????0000100000?????1001101102?????101010000000???00?000??001000000000  
10?0?????1?01????0?00?1???1??

Falcarius

??01?11100001111010?????1???00??????????00?????0000000??????100?000?0????  
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100101022030101010010001000000000000011000000000000?000?10?00?0?000?0?001000?  
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[01]0?????????0100020000?00000001110?1?0?0010000?001000000000010000???0100???000  
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Beipiaosaurus

0??1??10?10??????????  
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00?????????????????????????????????10000??????????1??0100??000000?0?0?0?0????0??  
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[illegible]

Erliansaurus

## Suzhousaurus

## Nothronychus

# Enigmosaurus

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Nanshiungosaurus\_brevispinus

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Therizinosaurus

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Haplocheirus

?0010???00010?0?12011011101112001?000020100?0?1010??0001?0010000010110110  
?1000001101010100??10?0?0111201??0?00001?0??0?00?????100210001210?0?00010??  
001?00?101002010010?011000?00000000?0000?0000000?00?1110001100010001?0??0010?  
01000000000?0000001?00000?102000000000????00??00??0??000000?0?0?0000?000?  
000????0????????????20000?000000010101?????100??000?00?????????0?00000?000  
0000?00?000100200000?????000?0?0?0??0100?000??0?0?????????00?0?????????0?0000  
001?00001??0?0000000?0?01000000?0??11??0?0?01??01?0???000001000000?00??100?00  
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Alvarezsaurus\_calvoi

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Patagonykus\_puertai

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0000?000?00?????0?0?0000?0?0010000???0?????????1??????????0???0???1002000000  
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001?101??1?0?1111111?????????????0?00000?0?????00?0000?00?0?00?1?????????10??1??  
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Achillesaurus

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Mononykus\_olecranus

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2?????00??????1?1?11102001???2?10?2?????1???1000?000200030210?02201100??1????1?20  
1000?2?????3??0??0210100111011212000030000001??00???1??0?0?00?0?0???00?????????  
?????????????????00011???0010?0?????210???00?  
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00000000000?0000?0?00?0?0?000??????01?0?????0?0??????11102????????????????????  
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000?????????1010100000100?????011???0???01?010000010101?100000100?????0???00?1?  
?0???021?111001011111111101011??????0100000000000?000?0000?000010000?000?10??  
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Shuvuuia\_deserti

?00101002?010111120110001011?01111?10020100001010010010???1110?001010010  
02100?0211??000?0111111011102100?0?201012012110100?1000?00020003021??02201100  
00101001?201000?2002203??03?02101001110112120000300000011000001100000010000?00  
??001000000001?010??000000000?000100000000?101000?10000110?0111000??0[12]0???01

## Parvicursor

## Albertonykus

## Albinykus

## Bonapartenykus

[illegible]

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Ceratomykus

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?0????????????????????00??????1????111????????????????????????????21?????0?????00  
00?0???01?????????????????????0??00000000?  
?000?000?00?0????????????????????1????10?0?????????????????0?0????????????????????????  
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???0?0??1000??????0?0??????????????????1?????1?00?0  
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Linhenykus

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??????????????0?1010001????2?2?0?030?0000???0???1??????????0?????0????????????????  
??????????01???0?0012?0?????210?????0?????20?  
?0???0?0?0????????????????????10000???0??????????31??????00?0?0?????????1?200000000000  
0?000?000?001?????0?0?????????1?????????0?????????????02????????????????????????  
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???1?????????????????????????????0?0?000?0?0??0000?0?00?0?0?????1?0?0??????????1011?????  
???1111?1???0?????????????????0?????????00??????????01?00?00001??????????0?1?110?0??  
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Xixianykus

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Nqwebasaurus

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Struthiomimus\_altus

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Gallimimus\_bullatus

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Garudimimus\_brevipes

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Pelecanimimus\_polydon

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Harpymimus\_okladnikovi

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Sinornithomimus

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[illegible]

Compsognathus\_longipes

Juravenator\_starki

# Sinocalliopteryx

## Mirischia

[illegible]

Ornitholestes hermanni

Coelurus\_fragilis

## Tanycolagreus

# Tugulusaurus

[illegible]

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Kileskus

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Guanlong

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# Sinotyrannus

Proceratosaurus\_bradleyi

Dilong\_paradoxus

Eotyrannus\_lengi

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Dryptosaurus

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Albertosaurus\_sacrophagus

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Gorgosaurus\_libratus

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Tarbosaurus\_baatar

## Uzbek Holotype Braincase Plus Referred Material

Uzbek Holotype Braincase Only

Uzbek Referred Material Only

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[illegible]

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